

# Movements and distribution of polar bears in the Beaufort Sea

S.C. Amstrup, G.M. Durner, I. Stirling, N.J. Lunn, and F. Messier

**Abstract:** We fitted 173 satellite radio collars (platform transmitter terminals) to 121 adult female polar bears in the Beaufort Sea and relocated the bears 44 736 times between 1985 and 1995. We regularly resighted many instrumented bears so that we could ascertain whether changes in movements or distribution were related to reproductive status. Mean short-term movement rates were less than 2 km/h for all classes of bears. Maximum movement rates occurred in winter and early summer. In the southern Beaufort Sea (SBS), net geographic movements from the beginning to the end of each month were smaller for females with cubs of the year than for solitary females, and larger in November than in April, May, or July. In May, June, July, and August, radio-collared bears in the SBS moved north. They moved south in October. In the northern Beaufort Sea (NBS), bears moved north in June and south in March and September. Total annual movements ranged from 1406 to 6203 km. Mean total distances moved each month ranged from 79 to 420 km. Total monthly movements by SBS bears were largest in early winter and smallest in early spring. In the NBS, movements were largest in summer and smallest in winter. In the SBS, females with cubs moved less each month than other females. Annual activity areas ranged from 7264 to 596 800 km<sup>2</sup>. Monthly activity areas ranged from 88 to 9760 km<sup>2</sup>. Seasonal fidelity to activity areas of bears captured in all parts of the Beaufort Sea was strongest in summer and weakest in spring.

**Résumé :** Nous avons installé 173 colliers émetteurs suivis par satellites (terminaux émetteurs de plateformes) à 121 ours blancs femelles adultes dans la mer de Beaufort et les avons repérés 44 736 fois entre 1985 et 1995. Nous avons revu plusieurs des ours munis d'instruments, ce qui nous a permis de confirmer si leurs déplacements ou leur répartition étaient reliés à leur statut reproducteur. Les taux moyens de déplacement à court terme étaient de moins de 2 km/h pour toutes les classes. Les taux de déplacement étaient maximaux en hiver et au début de l'été. Dans le sud de la mer de Beaufort (SBS), les déplacements géographiques nets du début à la fin de chaque mois étaient moins grands chez les femelles avec des petits de l'année que chez les femelles seules, et plus grands en novembre qu'en avril, mai ou juillet. En mai, juin, juillet et août, les ours du sud de la mer de Beaufort munis d'un émetteur se déplaçaient vers le nord. Ils se dirigeaient vers le sud en octobre. Dans le nord de la mer de Beaufort (NBS), les ours se déplaçaient vers le nord en juin et vers le sud en mars et septembre. Les déplacements annuels totaux se situaient entre 1406 et 6203 km. Les distances totales moyennes parcourues chaque mois allaient de 79 à 420 km. Les déplacements mensuels totaux des ours SBS étaient importants surtout au début de l'hiver et moins importants au début du printemps. Chez les ours NBS, les déplacements étaient plus importants en été et moins en hiver. Chez les ours SBS, les femelles avec petits se déplaçaient moins chaque mois que les autres femelles. Les zones d'activité annuelle allaient de 7264 à 596 800 km<sup>2</sup>. Les zones d'activité à l'échelle mensuelle allaient de 88 à 9760 km<sup>2</sup>. La fidélité saisonnière des ours capturés dans toute la mer de Beaufort était maximale en été et minimale au printemps.

[Traduit par la Rédaction]

## Introduction

Polar bears are distributed in several largely discrete subgroups (IUCN/SSC Polar Bear Specialists Group 1998) rather than constituting one homogeneous pan-Arctic population (Pedersen 1945). Seasonal and annual movement pat-

terns of individual polar bears likely vary among populations and little has been published regarding such patterns. Understanding the movement patterns of polar bears in each population is essential for minimizing the potential for detrimental effects from human activities such as hunting and industrialization of the Arctic.

In most populations, female polar bears keep their cubs for about 2.5 years before weaning, and mate every 3 years (DeMaster and Stirling 1981; Amstrup and DeMaster 1988; Ramsay and Stirling 1988). The nutritional demands on adult females change as the reproductive cycle progresses because cubs of different ages have differing total energy requirements. Hence, we reasoned that reproductive status (i.e., whether a female was alone or accompanied by cubs, and the age of those cubs) would affect their distribution and movements. Also, there are seasonal changes in the distribution and availability of ice habitat suitable for hunting for ringed seals (*Phoca hispida*) (Ferguson et al. 1998). There-

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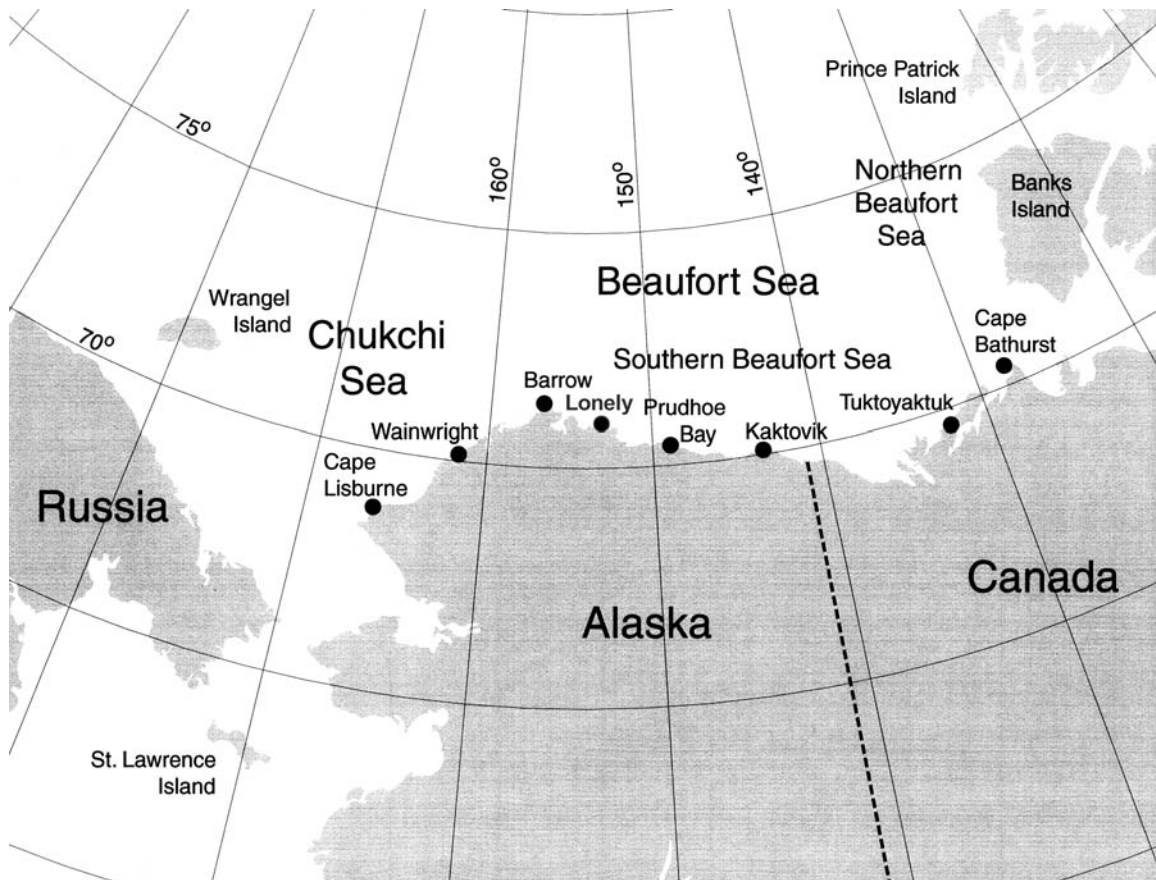
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**Fig. 1.** Map of northern Alaska and adjacent areas where polar bear marking and radio-tracking occurred, showing place names used in the text.



fore, we believed that movement patterns of polar bears might vary throughout the year. In this paper, we estimate and compare seasonal and annual movements of female polar bears that were either alone or accompanied by cubs of different ages in our study area, the Beaufort Sea.

## Materials and methods

### Field procedures

The Beaufort Sea extends from Point Barrow, Alaska, U.S.A., to Banks Island and Prince Patrick Island, Northwest Territories, Canada (Fig. 1). We captured polar bears by injecting immobilizing drugs (phencyclidine hydrochloride (Sernylan<sup>®</sup>, Park, Davis and Co.), etorphine hydrochloride (M-99<sup>®</sup>, Lemmon Co.), and tiletamine hydrochloride plus zolazepam hydrochloride (Telazol<sup>®</sup>, Warner-Lambert Co.) with projectile syringes fired from helicopters (Larsen 1971; Schweinsburg et al. 1982; Stirling et al. 1989). Capture protocols were approved by independent animal care and welfare committees. We captured and marked polar bears in the Beaufort Sea and adjacent areas each spring (except 1990) between 1985 and 1994, and in autumn of 1985, 1986, 1988, 1989, and 1994. Autumn captures were made in October and November each year and spring captures between March and May. In this report, we define bears captured along the north and west coast of Banks and Prince Patrick islands as northern Beaufort Sea (NBS) bears. This corresponds to the definition of the NBS in Bethke et al. (1996). Polar bears captured along the north coast of Alaska and northwest mainland Canada were called southern Beaufort Sea (SBS) bears.

Each year we attached radio transmitters to a sample of adult female polar bears. Beginning in 1985, we deployed radio collars equipped with ultra high frequency platform transmitter terminals (PTTs) that were relocated by ARGOS satellite. Although some PTTs transmitted daily, most transmitted for short periods (e.g., 4–8 h every 3–7 days). The high proportion of dormant time was designed to maximize battery life. Sensors on all PTTs recorded the temperature of the collar and two indices of activity. PTT-equipped polar bears also carried very high frequency beacons that we located with aircraft. We located radio-collared polar bears using position fixes from satellites, radio-tracking from aircraft, and with visual sightings. We used low frequency positioning devices (Loran-C, VLF-Omega) to record locations of polar bears observed by aircraft. Geographic locations of PTT-collared animals were determined by sensors on the satellite that interpreted frequency-shift patterns caused by changes in relative positions of the satellites and animals (Fancy et al. 1988). Data retrieved from PTTs were processed by the Argos Data Collection and Location System (Fancy et al. 1988).

### Analyses

Even though all data generated by PTTs and transmitted to the ARGOS satellites were available for analyses, we deleted all observations that were not in ARGOS classes 1 to 3 (i.e., the reported location may not have been within 1000 m of the animal's true location; Harris et al. 1990). Also, although we usually recorded multiple observations during each transmission day, for most analyses we deleted all but the one with the highest location quality.

We used Albers conic equal-area projection (Environmental Systems Research Institute (ESRI) 1992) for plotting recorded locations of radio-collared polar bears. In areas like the Beaufort

Sea that extend more in an east–west than north–south direction, Albers projected shapes have minimal distortion and are proportional to the same areas on the Earth (ESRI 1992). All locations of bears were recorded as latitude north and longitude west. For analyses, however, all geographic locations were converted to square Albers grid coordinates with a scale in metres. Hence, movements in all directions were measured on the same distance scale. We shifted the geographic center point of the Albers grid to ensure that all grid locations in our study area were positive. False easting and false northing values, therefore, were set to zero.

Instrumented females were classified according to whether they were solitary (not accompanied by young of any age), accompanied by cubs (aged <1 year), yearlings (aged 1–2 years), or 2-year-olds (aged 2–2.5 years). Females of all reproductive categories were not observed in all months. Hence, analyses were temporally subdivided. In most analyses, numbers of females with yearlings and solitary females could be compared throughout the year. Females with 2-year-olds were available for monitoring only between January and April of each year, and were compared with females with yearlings and solitary females during that time. Movement patterns of females with cubs, solitary females, and females with yearlings could only be compared for the period April–December. Comparisons of movements within each of these periods were accomplished with analysis of variance (ANOVA).

We used aircraft radiotelemetry to obtain visual observations of most SBS bears at intervals throughout the period during which they were instrumented. This allowed us to ascertain changes in reproductive status, such as bears emerging from dens with cubs or cubs surviving between years. This feature differentiates our study of polar bear movements from previous studies in which most animals were not resighted after being captured and radio-collared. In the Beaufort Sea, significant mortality of cubs has been documented between emergence from maternal dens and weaning (Amstrup and Durner 1995). Therefore, some bears that were suspected to have been accompanied by cubs of a particular age would have lost them. Hence, failure to resight bears to verify reproductive status can result in an unknown amount of error in reproductive-status classification. We hypothesized that reproductive status, as well as time of year, might influence measures of mobility (e.g., movement rates, net movement (shift in geographic position of each animal in each month), activity area). Therefore, we used a single-factor ANOVA to compare movements of bears whose reproductive status was confirmed with those whose status was only suspected. Because differences in movement patterns between suspected- and confirmed-status bears were usually significant, we limited our comparisons of SBS bears to animals whose status was confirmed.

Hourly movement rates were determined by measuring the linear distance between consecutive radiolocations and dividing by the number of hours separating those locations. We evaluated the effects of confirmed reproductive category and month on movements with three-factor ANOVA. Multiple comparisons among mean factor levels were made with the Tukey's Studentized range (HSD) test. Because we had numerous observations of each bear, we introduced an added factor, individual bear, into this and all other ANOVAs reported here. Use of individual bear as a factor allowed separation of the variability due to individuals from that associated with the factors of interest. Hence, the partial sums of squares due to variation among individual bears did not influence our hypothesis tests.

Net movement was defined as the linear distance between the first and last radiolocations recorded for each month. Total distance moved during the month was calculated for each bear by summing the distances (km) between consecutive satellite re-observations of the bear during that month. Total distance moved and net movement for each month were measured only if  $\geq 20$  days elapsed between the first and last radiolocations. We tested whether total

distance moved and total net movement were independent of month and reproductive category with three-factor ANOVA and Tukey's HSD test. Direction moved from the first to the last radiolocations for each month (mean azimuth and angular deviation or "dispersion" from the mean) was determined by converting angles to the appropriate trigonometric functions (Zar 1984, p. 422). We tested for significant directional tendencies by comparing azimuths of net movements for each month with Rayleigh's *Z* test of uniformity of distribution (Zar 1984, p. 443).

Total distance moved per year was calculated by summing the distances (km) between consecutive relocations for the whole year. Total annual distance moved was calculated only for bears that were monitored for  $\geq 292$  days (80% of a 365-day year). If a bear was monitored for  $> 365$  days, a second tracking year was designated. Similarly, if monitoring time exceeded 730 days, a third tracking year was designated. Tracking years did not coincide with a standardized calendar. Rather, they ran for 365 days beginning on the date of the first satellite observation for each bear. Gaps in relocation information of  $\geq 73$  days (20% of a monitoring year) were not allowed unless an animal occupied a maternal den during the gap in observations. Because the reproductive category of female polar bears changes during any year, we classified animals, for analyses of annual patterns, according to the most common (modal) category for each year of monitoring. We tested for differences in annual movements of bears in each category with two-factor ANOVA.

Areas used by polar bears were analyzed on monthly and annual bases. We calculated areas of annual activity only for bears that were monitored for  $\geq 292$  days, and for which there were at least 25 high-quality relocations. We used the same criteria for the start and finish of each year of monitoring as described for the calculation of annual movements. We calculated monthly activity areas for each month in which an individual bear generated  $\geq 8$  high-quality relocations over a period of  $\geq 20$  days within that month.

We used the program CALHOME V. 1.0 (Kie et al. 1996) for all activity-area calculations. Harmonic mean contours more closely approximated the observed distribution of re-observations of polar bears than did other methods that we evaluated. Therefore, we used the harmonic mean method (Dixon and Chapman 1980; Spencer and Barrett 1984; Lair 1987; Hayward et al. 1993) to compare activity areas among our polar bears. We also estimated convex polygon areas (Hayne 1949) to facilitate comparisons with earlier studies. We tested the null hypothesis that size of activity area is independent of reproductive category and month with three-factor ANOVA and Tukey's HSD test.

The size of an activity area can, theoretically, be underestimated if observations are temporally autocorrelated (Schoener 1981; Swihart and Slade 1985a, 1985b; Solow 1989). Autocorrelation of sequential observations was evaluated with the distribution-free multiresponse permutation procedure (Mielke et al. 1981; Biondini et al. 1988; Mielke 1991) in the sequence permutation (MRSP) subroutine of the program BLOSSOM (Slauson et al. 1991). We found significant autocorrelation, even when fewer than one location per month was considered. This apparent autocorrelation may have resulted from temporal and spatial clumping of data. Such clumping among relocations of radio-collared polar bears was neither seasonally nor annually predictable. It also varied among individuals in the same reproductive category. Hence, there was no way to minimize autocorrelation by partitioning the data. Because all animals were treated alike, however, any biases, whatever they may have been, were consistent and did not affect comparisons among animals or time periods.

We examined monthly fidelity of polar bears to activity areas by comparing harmonic mean centers of activity (Dixon and Chapman 1980) for bears observed in the same month during different years. When an individual female completes a successful reproductive cycle, each reproductive category will occur only once every 3 years.

**Table 1.** Movement rates (km/h) of female polar bears radio-collared in the southern and northern Beaufort seas, 1985–1995.

	Southern Beaufort Sea				Northern Beaufort Sea			
	Solitary females	Females with cubs	Females with yearlings	Females with 2-year-olds	Solitary females	Females with cubs	Females with yearlings	Females with 2-year-olds
Periods ≤8 h								
Mean	1.93	1.86	1.86	1.78	1.99	2.07	1.97	2.03
Min.	0.02	0.02	0.01	0.02	0	0.09	0	0.65
Max.	9.51	9.47	9.79	7.24	9.54	8.88	8.82	4.08
SD	1.52	1.47	1.43	1.39	1.72	1.51	1.48	1.11
5% quantile	0.24	0.26	0.25	0.24	0.17	0.36	0.29	0.65
25% quantile	0.75	0.76	0.77	0.73	0.71	0.92	0.88	1.09
Median	1.56	1.48	1.51	1.42	1.57	1.71	1.56	1.62
75% quantile	2.73	2.56	2.63	2.48	2.69	2.89	2.62	3.19
95% quantile	4.82	4.66	4.44	4.73	5.43	4.71	4.94	4.08
Periods >8 and ≤168 h								
Mean	0.64	0.57	0.64	0.47	0.46	0.58	0.48	0.33
Min.	0	0	0.01	0.01	0.01	0	0.02	0.07
Max.	4.79	4.34	3.90	3.28	4.79	2.80	3.39	1.18
SD	0.54	0.58	0.56	0.45	0.50	0.46	0.45	0.27
5% quantile	0.09	0.07	0.06	0.07	0.03	0.09	0.05	0.07
25% quantile	0.28	0.22	0.25	0.18	0.17	0.25	0.18	0.12
Median	0.51	0.39	0.50	0.31	0.33	0.47	0.35	0.22
75% quantile	0.85	0.73	0.86	0.62	0.62	0.74	0.61	0.39
95% quantile	1.63	1.67	1.76	1.50	1.17	1.59	1.37	0.87

**Note:** The reproductive status of bears in the northern Beaufort Sea was not confirmed.

Hence, sample sizes were insufficient to evaluate monthly fidelity according to reproductive category. Therefore, the hypothesis that fidelity to activity areas is independent of month was tested with two-factor ANOVA and Tukey's HSD test.

In the SBS, where we deployed the largest number of radios, we compared relocations of bears with their original capture locations to assess fidelity and geographic-use patterns. We analyzed captures and recaptures made in the area from western Canada to the Chukchi Sea west of Alaska. We combined locations of all bears originally captured in 3 longitude zones 10° wide between longitudes 137° and 167°. We also combined locations of all bears captured in two other capture zones: east of 137° and west of 167°. We assumed that these noncorrelated samples from individuals observed on different days and under differing environmental conditions represented independent samples of spatial-use patterns.

We held Tukey's HSD family confidence levels at  $P = 0.05$  in all ANOVAs. We rejected the null hypotheses of our other statistical tests at  $P = 0.05$ , but we report actual probabilities unless  $P < 0.001$ . We performed statistical analyses on a Unix workstation running SAS version 6.11 software (SAS Institute, Inc., Cary, N.C.), and on a Pentium personal computer running Excel (Microsoft Corp., Redmond, Wash.) and SPSS version 6.1 software (SPSS Inc., Chicago, Ill.). Our criteria for different analyses were not identical (e.g., rates of hourly movement were not limited to months with at least 20 days of tracking). Therefore, despite our best efforts to standardize analytical rules, sample sizes varied among different categories of analyses.

## Results

We deployed 152 PTTs on 104 adult female polar bears along the mainland coast of the Beaufort Sea (SBS) and obtained 39 554 location records between May 1985 and December 1994. We also deployed 21 PTTs on 17 polar bears along the north and west coast of Banks Island and the west

coast of Prince Patrick Island (NBS). Those PTTs provided 6568 location records between April 1989 and December 1995. After we excluded multiple daily locations and those with inadequate precision, we were left with 12 267 location records from the Beaufort Sea that form the basis of most results reported here.

Rates of movement for females with cubs in the SBS were significantly lower than those of females suspected to have cubs ( $F_{[1]} = 11.00$ ,  $P < 0.0001$ ), and rates of females with 2-year-olds were lower than those of females suspected to have 2-year-olds ( $F_{[1]} = 4.35$ ,  $P = 0.04$ ). Although the difference was not significant, females with yearlings appeared to move more slowly than those suspected to have yearlings. Similar differences were apparent for other measurements of movement. Hence, unless otherwise specified, the SBS samples used in our analyses include only animals whose status was confirmed. Smaller sample sizes in the NBS mandated that all animals be used in comparisons whether their reproductive status was verified or not.

## Movements

### *Movement rates*

Hourly movement rates of SBS and NBS bears were nearly statistically different ( $F_{[1]} = 3.65$ ,  $P = 0.06$ ), but not practically different (Table 1). The duty cycles of our PTTs allowed us to evaluate movement rates at intervals of 0–8, 8–20, 20–28, 68–100, and 100+ h. Corresponding movement rates, averaged over both populations were 1.82, 0.89, 0.67, 0.55, and 0.41 km/h. Declines in movement rates with increasing time were highly significant ( $F_{[4]} = 741$ ,  $P < 0.0001$ ). Because of the large drop in hourly movements for

**Table 2.** Movement rates (km/h) of satellite-radio-collared female polar bears in the southern Beaufort Sea, 1985–1995.

	Females with cubs			Solitary females			Females with yearlings			Females with 2-year-olds			Monthly total			Significantly different at $P = 0.05$
	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	
March				1.54	0.14	131	1.39	0.09	186	1.66	0.12	118	1.51	0.06	435	
April				1.86	0.08	475	1.58	0.08	254	1.66	0.10	150	1.75	0.05	879	
February							2.01	0.12	139	1.77	0.13	125	1.90	0.09	264	
January							1.92	0.09	230	2.12	0.15	101	1.98 <sup>a</sup>	0.08	331	
Total				1.80	0.07	606	1.71	0.05	809	1.78	0.06	494				
September	1.58	0.17	86	1.41	0.06	350	1.52	0.11	85				1.46	0.05	521	
April	1.43	0.07	309	1.86	0.08	475	1.58	0.08	254				1.66	0.05	1038	
October	1.85	0.12	152	1.62	0.07	407	1.65	0.11	167				1.68	0.05	726	
May	1.74	0.10	165	1.82	0.05	988	1.76	0.09	236				1.80	0.04	1389	
August	1.87	0.17	71	1.88	0.08	349	1.77	0.13	100				1.86	0.06	520	
December	1.95	0.08	375	1.39	0.37	4	2.06	0.09	354				2.00	0.06	733	
November	2.16	0.09	327	2.32	0.10	308	1.97	0.08	318				2.15	0.05	953	
June	2.20	0.14	101	2.26	0.05	710	2.25	0.11	160				2.25	0.05	971	
July	2.03	0.15	83	2.35	0.08	421	2.22	0.11	137				2.28 <sup>b</sup>	0.06	641	
Total	1.86	0.04	1669	1.95	0.02	4012	1.89	0.03	1811							
September				1.41	0.06	350	1.52	0.11	85				1.43	0.05	435	
March				1.54	0.14	131	1.39	0.09	186				1.45	0.08	317	
October				1.62	0.07	407	1.65	0.11	167				1.63	0.06	574	
April				1.86	0.08	475	1.58	0.08	254				1.77	0.06	729	
May				1.82	0.05	988	1.76	0.09	236				1.81	0.04	1224	
August				1.88	0.08	349	1.77	0.13	100				1.86	0.07	449	
January							1.92	0.09	230				1.92	0.09	230	
February							2.01	0.12	139				2.01	0.12	139	
December				1.39	0.37	4	2.06	0.09	354				2.05	0.09	358	
November				2.32	0.10	308	1.97	0.08	318				2.14	0.06	626	
June				2.26	0.05	710	2.25	0.11	160				2.26	0.05	870	
July				2.35	0.08	421	2.22	0.11	137				2.32 <sup>c</sup>	0.07	558	
Total				1.93 <sup>d</sup>	0.02	4143	1.86	0.03	2366							

**Note:** Movement rates were calculated only if the re-observation interval was less than 8 h. Significant differences among months (Tukey's HSD test) are indicated by non-overlapping lines. *N* is the number of measurements of rates of movement.

<sup>a</sup> $F_{[3]} = 6.89, P < 0.001$ ; HSD = 3.32,  $df = 1834, P = 0.05$ .

<sup>b</sup> $F_{[8]} = 12.56, P < 0.001$ ; HSD = 4.39,  $df = 7376, P = 0.05$ .

<sup>c</sup> $F_{[11]} = 12.5, P < 0.001$ ; HSD = 4.63,  $df = 6406, P = 0.05$ .

<sup>d</sup>Solitary females moved at a faster rate than females with yearlings ( $F_{[1]} = 6.95, P = 0.0084$ ; HSD = 2.77,  $df = 6406, P = 0.05$ ).

**Table 3.** Movement rates (km/h) of satellite radio-collared female polar bears in the northern Beaufort Sea, 1989–1995.

	Females with cubs			Solitary females			Females with yearlings			Females with 2-year-olds			Monthly total		
	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>
January							1.39	0.20	38	1.28	0.35	2	1.38	0.19	40
April				1.56	0.46	15	1.66	0.24	26	2.26	0.64	5	1.70	0.21	46
February							1.90	0.20	41	1.62		1	1.89	0.19	42
March							2.00	0.22	36	2.28	0.60	3	2.02	0.20	39
Total				1.56	0.46	15	1.74	0.11	141	2.03	0.33	11			
September	1.85	0.26	37	1.37	0.18	24	1.84	0.41	12				1.69	0.16	73
November	1.76	0.19	54				4.29	3.05	2				1.85	0.21	56
October	1.96	0.21	56	2.03	0.54	10	1.03	0.41	6				1.89	0.19	72
April	2.56	0.44	24	1.56	0.46	15	1.66	0.24	26				1.97	0.22	65
May	2.02	0.15	99	2.03	0.25	41	2.26	0.36	25				2.06	0.12	165
July	2.00	0.12	144	2.34	0.31	39	2.51	0.44	20				2.12	0.11	203
August	2.15	0.13	132	2.02	0.32	30	2.44	0.38	14				2.15	0.12	176
June	2.18	0.15	96	2.12	0.32	38	2.32	0.30	16				2.18	0.13	150
December	2.30	0.20	48				3.35	1.27	3				2.36	0.20	51
Total	2.07	0.06	690	1.99	0.12	197	2.16	0.15	124						
January							1.39	0.20	38				1.39	0.20	38
September				1.37	0.18	24	1.84	0.41	12				1.53	0.18	36
April				1.56	0.46	15	1.66	0.24	26				1.63	0.23	41
October				2.03	0.54	10	1.03	0.41	6				1.65	0.38	16
February							1.90	0.20	41				1.90	0.20	41
March							2.00	0.22	36				2.00	0.22	36
May				2.03	0.25	41	2.26	0.36	25				2.12	0.20	66
August				2.02	0.32	30	2.44	0.38	14				2.15	0.25	44
June				2.12	0.32	38	2.32	0.30	16				2.18	0.24	54
July				2.34	0.31	39	2.51	0.44	20				2.40	0.25	59
December							3.35	1.27	3				3.35	1.27	3
November							4.29	3.05	2				4.29	3.05	2
Total				1.99	0.12	197	1.97	0.10	239						

**Note:** Movement rates were calculated only if the re-observation interval was less than 8 h. There were no significant differences (Tukey's HSD test) among months or reproductive-status categories. *N* is the number of measurements of rates of movement.

all periods greater than 8 h, we combined these longer periods for subsequent evaluation (Table 1).

Maximum movement rates recorded over periods of time ranging from 1 to 8 h approached 10 km/h in both the NBS and the SBS. Polar bears were capable of making very long movements over short periods of time, and sometimes maintained high movement rates for long periods. Several animals sustained movement rates >4 km/h for >20 h. One bear moved at 4.3 km/h for 45 h, another moved at 4.5 km/h for >41 h, and a third moved 4.0 km/h for 46 h. Maximum movement rates must have exceeded these because we suspect that bears seldom moved along the straight lines we recorded. Mean rates of short-term movement were less than 2 km/h for all classes of bears, however (Table 1). Mean rates of movement measured over time intervals >8 h were smaller still (Table 1).

In the SBS, hourly movement rates (measured for periods ≤8 h) varied greatly among months (Table 2). The highest movement rates were measured in early summer and winter. The lowest rates were measured in autumn and spring. In the NBS there were no significant differences among months or reproductive classes (Table 3). Temporal patterns in movement rates of bears in the NBS did appear similar to those of

bears in the SBS. The ability to detect temporal patterns, however, may have been hampered by small numbers of measurements in the NBS.

#### Net monthly movements

There were few significant variations in net movement among months or reproductive categories for bears in the SBS (Table 4). Net distances between the first and the last radiolocations each month were shorter for females with cubs than for solitary females ( $F_{[2]} = 5.06$ ,  $P = 0.007$ ; HSD = 3.32,  $df = 535$ ,  $P = 0.05$ ). For the months April–December, net movements in November, averaged over all bears, were greater than they were in April, May, or July ( $F_{[8]} = 2.79$ ,  $P = 0.005$ ; HSD = 4.41,  $df = 535$ ,  $P = 0.05$ ). Likewise, when solitary females and females with yearlings were considered over all months, net November movements exceeded those in March and April ( $F_{[11]} = 2.47$ ,  $P = 0.005$ ; HSD = 4.64,  $df = 504$ ,  $P = 0.05$ ). Other differences between reproductive category and month were not significant, and there were no significant interactions.

In the NBS, we observed no differences in net monthly movement among reproductive categories ( $P \geq 0.57$  in all cases) or among months ( $P \geq 0.1$  in all cases). It is notable,

**Table 4.** Net movement (km) from first to last locations each month for satellite radio-collared female polar bears in the southern Beaufort Sea, 1985–1995. Significant differences among reproductive classes are noted below.

	Females with cubs			Solitary females			Females with yearlings			Females with 2-year-olds			Monthly total			Significantly different at $P = 0.05$
	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	
March				153	29	14	74	11	9	140	60	12	128	24	35	
April				141	14	31	112	29	13	112	20	9	129	11	53	
February				166	37	8	162	37	7	102	23	14	134	18	29	
January				285	98	12	185	64	10	131	30	14	197	39	36	
Total				173	21	65	131	21	39	121	18	49				
April	79	14	10	141	14	31	112	29	13				123	11	54	
May	134	21	13	160	13	84	149	25	18				155	10	115	
July	112	19	9	154	10	68	191	32	16				156	9	93	
December	139	36	12	137	55	12	172	34	16				152 <sup>a</sup>	23	40	
September	156	31	10	170	15	49	147	57	8				165	13	67	
October	149	37	9	188	26	31	120	24	12				165	18	52	
June	86	21	11	192	17	69	121	25	15				168	14	95	
August	115	27	11	185	14	54	183	28	14				175	12	79	
November	200	41	14	256	38	17	223	42	17				228 <sup>b</sup>	23	48	
Total	133 <sup>c</sup>	10	99	172	6	415	161	11	129							
March				153	29	14	74	11	9				122	19	23	
April				141	14	31	112	29	13				132	13	44	
December				137	55	12	172	34	16				157	30	28	
May				160	13	84	149	25	18				158	11	102	
July				154	10	68	191	32	16				161	10	84	
February				166	37	8	162	37	7				164	25	15	
September				170	15	49	147	57	8				167	15	57	
October				188	26	31	120	24	12				169	20	43	
June				192	17	69	121	25	15				179	15	84	
August				185	14	54	183	28	14				184	12	68	
January				285	98	12	185	64	10				239	61	22	
November				256	38	17	223	42	17				240 <sup>d</sup>	28	34	
Total				175	6	449	157	10	155							

**Note:** *N* is the number of bears in each reproductive category sampled each month. Lines in the final column overlap months in which net movements did not differ significantly. All pairwise significance levels were determined by Tukey's HSD test.

<sup>a</sup>The lack of significance is apparently due to the SE and sample size considerations.

<sup>b</sup> $F_{[8]} = 2.79$ ,  $P = 0.005$ ; HSD = 4.41,  $df = 535$ ,  $P = 0.05$ .

<sup>c</sup>Females with cubs moved shorter distances from the beginning to the end of each month than solitary females ( $F_{[2]} = 5.06$ ,  $P = 0.007$ ; HSD = 3.32,  $df = 535$ ,  $P = 0.05$ ).

<sup>d</sup> $F_{[11]} = 2.47$ ,  $P = 0.005$ ; HSD = 4.64,  $df = 504$ ,  $P = 0.05$ .

however, that the greatest net movements among NBS bears occurred in April and May (Table 5), whereas net movements of SBS bears were consistently low during those months (Table 4).

The azimuths of net monthly movements recorded for instrumented SBS polar bears were not independent of the month of measurement (Table 6). In February, March, April, September, November, and December, directions of polar bear movements were highly variable, and uniformly distributed around the compass rose. In January, however, the average net polar bear movement was easterly, and the distribution of azimuths was significantly different from uniform. In May, June, July, and August, net movements of polar bears deviated from uniformity, all being in northerly directions, and in October, polar bears moved significantly south (Table 6).

In January, February, April, July, August, November, and December, directions of polar bear movements in the NBS were highly variable (Table 7). Net movements in March were to the southwest in a pattern that was almost significant, and in June, polar bears moved north. In September, they moved significantly south and southwest. Hence, we noted differences between the NBS and SBS in direction as well as distance of net movement from the beginning to the end of each month.

#### Total distances

Total annual travel distances varied greatly among individual bears but not among categories of bears. Even when bears that entered maternity dens were included, variation in annual distance moved was not related to reproductive status of bears in either the SBS ( $F_{[3]} = 0.52$ ,  $P = 0.67$ ) or the NBS

**Table 5.** Net movement (km) from first to last locations each month for satellite-radio-collared female polar bears in the northern Beaufort Sea, 1989–1995.

	Females with cubs			Solitary females			Females with yearlings			Females with 2-year-olds			Monthly total		
	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>
February				113	18	3	94	23	9	16	9	4	78	16	16
March				92	18	4	90	18	11	77	33	4	88	13	19
January				199	153	3	93	26	10	50	36	6	96	29	19
April				140	13	6	142	61	8	102	35	4	133	28	18
Total				134	27	16	103	16	38	60	17	18			
December	105	17	11	54	17	2	47	14	6				81	13	19
November	81	10	13	103	28	3	128	42	5				95	12	21
September	128	26	13	83	23	12	98	21	6				105	15	31
October	106	26	14	62	19	5	163	67	5				109	21	24
August	89	18	14	132	49	13	141	52	7				116	22	34
July	128	22	15	112	20	17	141	65	7				123	16	39
June	129	25	15	107	18	16	158	40	6				124	14	37
April	84	38	5	140	13	6	142	61	8				126	27	19
May	139	29	16	158	26	16	113	31	8				141	17	40
Total	113	8	116	116	10	90	126	16	58						
December				54	17	2	47	14	6				49	11	8
September				83	23	12	98	21	6				88	16	18
March				92	18	4	90	18	11				91	14	15
February				113	18	3	94	23	9				99	18	12
October				62	19	5	163	67	5				113	37	10
January				199	153	3	93	26	10				117	38	13
November				103	28	3	128	42	5				118	27	8
July				112	20	17	141	65	7				121	23	24
June				107	18	16	158	40	6				121	17	22
August				132	49	13	141	52	7				135	36	20
April				140	13	6	142	61	8				141	34	14
May				158	26	16	113	31	8				143	20	24
Total				117	10	100	114	11	88						

**Note:** *N* is the number of bears in each reproductive category sampled each month. There were no significant differences among reproductive classes of bears or among months. All pairwise comparisons were made by Tukey's HSD test.

**Table 6.** Mean azimuths (degrees true) and angular deviations (degrees; Zar 1984) of net movements from the beginning to the end of each month for satellite-radio-collared female polar bears in the southern Beaufort Sea.

	Mean azimuth of displacement	Angular deviation	<i>Z</i>	<i>P</i>	No. of animals
January	72	67.8	5.59	<0.005	62
February	99	76.0	0.73	0.5	51
March	140	78.1	0.35	>0.50	69
April	251	76.4	1.10	>0.20	89
May	20	72.4	5.05	<0.01	123
June	6	72.9	4.03	<0.01	112
July	325	66.2	11.48	<0.001	104
August	42	71.0	4.77	<0.01	89
September	58	74.0	2.12	>0.10	76
October	199	68.7	5.42	<0.005	69
November	215	75.5	1.23	>0.20	70
December	323	78.8	0.19	>0.50	64

**Note:** All reproductive categories are combined. Large values for Rayleigh's *Z* test indicate a significant trend in monthly mean azimuth (Zar 1984).



**Table 7.** Mean azimuths (degrees true) and angular deviations (degrees; Zar 1984) of net movements from the beginning to the end of each month for satellite-radio-collared female polar bears in the northern Beaufort Sea.

	Mean azimuth of displacement	Angular deviation	Z	P	No. of animals
January	89	71.7	0.66	>0.5	14
February	229	71.1	0.74	>0.2	14
March	240	63.0	2.51	0.08	16
April	143	78.0	0.09	>0.5	16
May	220	71.0	1.79	>0.1	33
June	343	67.7	2.93	0.05	32
July	14	72.9	1.16	>0.5	32
August	33	76.6	0.31	>0.5	27
September	212	48.8	10.55	<0.001	26
October	244	67.5	2.25	>0.1	24
November	177	79.1	0.04	>0.5	18
December	251	79.1	0.04	>0.5	16

**Note:** All reproductive categories are combined. Large values for Rayleigh's Z test indicate a significant trend in monthly mean azimuth (Zar 1984).

( $F_{[3]} = 1.80$ ,  $P = 0.25$ ). In the SBS, mean annual movements were 3087, 3409, and 3917 km for females with cubs, solitary females, and females with yearlings, respectively. Corresponding mean annual movements of bears in the NBS were 2855, 2360, and 2552 km, respectively. Solitary females accounted for both the largest (6203 km) and smallest (1454 km) annual movements in the SBS. A female with new cubs made the longest recorded annual movement (3848 km) in the NBS, while a solitary female made the shortest (1406 km) annual movement. In the NBS, only 5 females with yearlings and 3 solitary females were followed for a full year. These small samples, and the fact that the status of most instrumented bears there was not verified, probably contributed to the observed differences in patterns of annual movements between the NBS and SBS.

Although they did not differ on an annual basis, total travel distances varied among months and reproductive categories in both the SBS and NBS (Tables 8 and 9). Between April and December, females in the SBS moved shorter distances each month when they were accompanied by cubs than when they were solitary or accompanied by yearlings ( $F_{[2]} = 4.46$ ,  $P = 0.012$ ; HSD = 3.32, df = 535,  $P = 0.05$ ). During this period, distances moved were greatest in November, exceeding those for April, May, and July ( $F_{[8]} = 2.32$ ,  $P = 0.018$ ; HSD = 4.41, df = 535,  $P = 0.05$ ). Movements in December also exceeded those in April and May. For January through December, the period for which females with yearlings and solitary females could be compared, movements in November exceeded those in March, April, May, and July (Table 8). Also, total movements in December and June exceeded those in March ( $F_{[11]} = 2.91$ ,  $P = 0.001$ ; HSD = 4.64, df = 504,  $P = 0.05$ ). Other differences among months and classes of female were not significant, and there were no interactions.

In the NBS there were no significant differences in movements among female polar bears of different reproductive status and few differences among months (Table 9). Between January and April, when solitary females and females with yearlings or two-year-olds could be compared, movements in April exceeded those in all other months. Although the

differences were large, they were not significant ( $F_{[3]} = 1.67$ ,  $P = 0.19$ ), apparently because of small sample sizes and differing variances. Total distances moved by solitary females and those with cubs or yearlings during the period April–December were largest in May and July (Table 9). Movements during May and July exceeded those for December ( $F_{[8]} = 2.73$ ,  $P = 0.007$ ; HSD = 4.43, df = 220,  $P = 0.05$ ). For the period January–December, when females with yearlings and solitary females could be compared, distances moved in May exceeded those in December ( $F_{[11]} = 1.71$ ,  $P = 0.076$ ; HSD = 4.70, df = 145,  $P = 0.05$ ). No significant interactions between month and status were noted during any of the time periods evaluated.

### Spatial use patterns

#### Activity areas

We calculated 75 annual activity areas for 57 PTT-equipped polar bears in the SBS and 29 activity areas for 18 bears in the NBS. Estimates of activity areas were derived from 29–166 ( $\bar{x} = 69$ ) satellite relocations in the SBS and 29–118 ( $\bar{x} = 69$ ) relocations in the NBS. Contours developed by the harmonic mean method provided the best fit to actual observations. Most contours estimated for individual bears included only sea-ice habitats and small portions of land near den locations (Fig. 2). Annual activity areas (95% harmonic mean contours) of female polar bears were significantly larger in the SBS than in the NBS ( $F_{[1]} = 8.61$ ,  $P = 0.004$ ). Areas occupied ranged between 12 730 and 596 800 km<sup>2</sup> in the SBS. Those in the NBS ranged between 7264 and 201 200 km<sup>2</sup>. Only the top 25% of radio-collared bears occupied activity areas  $\geq 188 000$  km<sup>2</sup> in the SBS and  $\geq 113 300$  km<sup>2</sup> in the NBS (Table 10).

Differences in activity-area sizes among bears that varied in reproductive status were not significant in either the NBS ( $F_{[3]} = 1.42$ ,  $P = 0.308$ ) or the SBS ( $F_{[3]} = 0.51$ ,  $P = 0.679$ ) (Table 11). The sizes and locations of the annual activity areas of some individual bears varied considerably among years (Fig. 2), indicating that multiple years of monitoring

**Table 8.** Total distances (km) moved per month by satellite-radio-collared female polar bears varying in reproductive status in the southern Beaufort Sea, 1985–1995.

	Females with cubs			Solitary females			Females with yearlings			Females with 2-year-olds			Monthly total			Significantly different at $P = 0.05$
	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	
March				248	30	14	178	30	9	251	73	12	231	28	35	
February				331	91	8	235	37	7	192	24	14	241	30	29	
April				255	25	31	274	42	13	214	36	9	252	19	53	
January				301	64	12	309	61	10	228	28	14	275	29	36	
Total				271	21	65	254	24	39	221	21	49				
April	192	44	10	255	25	31	274	42	13				248	19	54	
May	237	22	13	293	15	84	259	27	18				281	12	115	
July	243	51	9	288	14	68	314	33	16				288	13	93	
September	241	25	10	296	20	49	279	59	8				286 <sup>a</sup>	16	67	
October	270	40	9	335	27	31	240	41	12				302	20	52	
August	220	24	11	315	17	54	322	43	14				303	15	79	
June	173	22	11	340	17	69	284	25	15				312	14	95	
December	381	73	12	345	78	12	369	57	16				365	39	40	
November	320	44	14	420	34	17	355	48	17				368 <sup>b</sup>	25	48	
Total	256 <sup>c</sup>	15	99	310	7	415	303	14	129							
March				248	30	14	178	30	9				220	22	23	
April				255	25	31	274	42	13				260	21	44	
May				293	15	84	259	27	18				287	13	102	
July				288	14	68	314	33	16				293	13	84	
February				331	91	8	235	37	7				286 <sup>a</sup>	51	15	
September				296	20	49	279	59	8				294	19	57	
January				301	64	12	309	61	10				305	44	22	
October				335	27	31	240	41	12				308	23	43	
August				315	17	54	322	43	14				316	16	68	
June				340	17	69	284	25	15				330	15	84	
December				345	78	12	369	57	16				358	46	28	
November				420	34	17	355	48	17				388 <sup>d</sup>	30	34	
Total				308	7	449	293	13	155							

**Note:** *N* is the number of bears of each status sampled each month. The line in the last column overlaps months in which movements did not differ significantly. All pairwise significance levels were determined by Tukey's HSD test.

<sup>a</sup>The lack of significance is apparently due to the SE and sample-size considerations.

<sup>b</sup> $F_{[8]} = 2.32, P = 0.018; HSD = 4.41, df = 535, P = 0.05.$

<sup>c</sup>Females with cubs moved shorter distances each month than other females ( $F_{[2]} = 4.46, P = 0.012; HSD = 3.32, df = 535, P = 0.05).$

<sup>d</sup> $F_{[11]} = 2.91, P = 0.001; HSD = 4.64, df = 504, P = 0.05.$

allow a greater understanding of the geographic distribution of polar bears than any individual year.

We estimated 332 monthly activity areas for 72 SBS polar bears that were not in dens, and whose reproductive category was known. Which areas were occupied appeared to depend upon month and reproductive category. Three-factor ANOVAs, performed for time periods when bears of each reproductive category were present, showed that only differences among months were significant. Therefore, data from all animals of known category were pooled to examine overall monthly differences with a two-factor ANOVA. That analysis confirmed that 95% contour areas occupied in December exceeded those in all other months ( $F_{[11]} = 2.61, P < 0.004; HSD = 4.67, df = 249, P = 0.05).$  Other differences were not significant (Table 12).

We estimated 101 monthly activity areas for 17 NBS polar bears. Reproductive category was not confirmed for these

bears. Three-factor ANOVAs, performed for time periods when bears of each reproductive category were present, showed no significant differences among months or reproductive classes. When data were pooled over all reproductive categories, a two-factor ANOVA indicated no differences among any months ( $F_{[11]} = 0.68, P < 0.76)$  (Table 12).

*Geographic patterns*

Bears captured along the mainland coast of the Beaufort Sea did not utilize all Beaufort Sea areas equally. After capture, bears tended to move west from the far-eastern Beaufort Sea. Only 8% of relocations of bears captured and radio-collared near Tuktoyaktuk, N.W.T. (from longitude 127° to 137°), were recorded east of 127°, and only 17% were recorded between 127° and 137°. The remaining 75% of the relocations of bears captured near Tuktoyaktuk were west of 137°. Of bears captured near Kaktovik (137°–

**Table 9.** Total distances (km) moved per month by satellite-radio-collared female polar bears varying in reproductive status in the northern Beaufort Sea, 1989–1995.

	Females with cubs			Solitary females			Females with yearlings			Females with 2-year-olds			Monthly total			Significantly different at $P = 0.05$
	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	
February				140	26	3	142	30	9	55	21	4	120	20	16	
January				214	155	3	133	27	10	97	39	6	134	29	19	
March				189	58	4	156	21	11	136	45	4	159	19	19	
April				241	32	6	248	75	8	160	24	4	226	35	18	
Total				204	32	16	166	20	38	110	19	18				
December	186	28	11	79	25	2	110	27	6				151	20	19	
November	167	21	13	170	11	3	219	51	5				180	18	21	
September	201	24	13	151	36	12	240	81	6				189	23	31	
April	146	48	5	241	32	6	248	75	8				219	35	19	
October	221	32	14	217	36	5	222	63	5				220	23	24	
June	215	26	15	268	25	16	254	37	6				244	16	37	
August	217	21	14	270	69	13	261	47	7				246	29	34	
May	225	31	16	300	33	16	262	33	8				263	19	40	
July	269	27	15	252	24	17	277	61	7				263 <sup>a</sup>	18	39	
Total	212	9	116	243	15	90	236	19	58							
December				79	25	2	110	27	6				102	21	8	
February				140	26	3	142	30	9				142	23	12	
January				214	155	3	133	27	10				152	38	13	
March				189	58	4	156	21	11				165	21	15	
September				151	36	12	240	81	6				181	36	18	
November				170	11	3	219	51	5				201	32	8	
October				217	36	5	222	63	5				220	34	10	
April				241	32	6	248	75	8				245	44	14	
July				252	24	17	277	61	7				260	24	24	
June				268	25	16	254	37	6				264	21	22	
August				270	69	13	261	47	7				267	47	20	
May				300	33	16	262	33	8				288 <sup>b</sup>	24	24	
Total				237	14	100	205	14	88							

**Note:** *N* is the number of bears of each status sampled each month. The line in the last column overlaps months in which movements did not differ significantly. All pairwise significance levels were determined by Tukey's HSD test.

<sup>a</sup> $F_{[8]} = 2.52$ ,  $P = 0.012$ ; HSD = 4.43,  $df = 216$ ,  $P = 0.05$ .

<sup>b</sup> $F_{[8]} = 2.32$ ,  $P = 0.018$ ; HSD = 4.70,  $df = 145$ ,  $P = 0.05$ .

147°W), 46% were re-observed there and 47% were re-observed west of 147°. Only 7% were observed east of 137°, providing further evidence for a tendency of bears captured in the eastern SBS to move west. Bears captured between longitudes 147° and 157° were relocated equally east and west of their capture locales.

#### Philopatry

Bears in the SBS showed significant differences in fidelity to monthly activity areas ( $F_{[11]} = 7.84$ ,  $P < 0.001$ ). They were most faithful to their July activity areas. In July, activity centers used in one year were only 199 km from those used in other years (Table 13). SBS bears were least faithful to March activity areas, which were 450 km apart. Fidelity tended to be strongest in summer and early autumn and weakest in winter and early spring. Fidelity patterns among

NBS bears were similar. Fidelity was strongest there in August and weakest in March (Table 13).

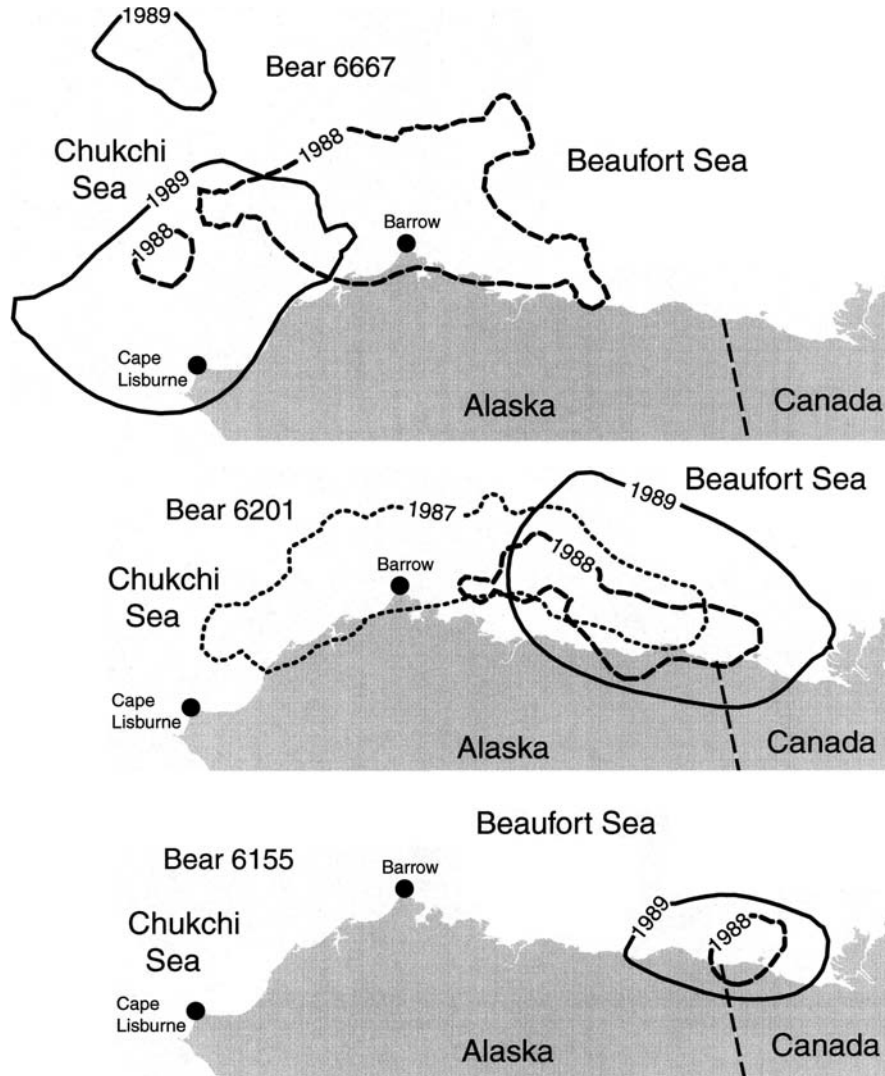
## Discussion

### Movements

#### Movement rates

Recorded movement rates differed from reality because bears do not move in a straight line and because the ice of the Beaufort Sea is constantly moving. We observed that polar bears occupying dens built upon the pack ice drifted up to 0.7 km/h, and that the average westerly drift was 0.15 km/h between November and March. Hence, rates of movement relative to the ice surface could have been lower than we recorded if bears were traveling to the west, and some bears walking eastward could actually have been dis-

**Fig. 2.** Sample activity-area boundaries for 3 female polar bears followed by satellite radiotelemetry in 1988 and 1989. Note the overlap in activity areas among years and the variation in sizes of areas occupied among individuals. The 1987 activity area of female 6201 and the activity areas for female 6667 illustrate that variation and overlap in areas among years is a common trait of polar bear activity areas.



placed to the west (Table 1). Bears walking to the east would have had to walk 0.15 km/h, on average, simply to stay in the same place. Average movements of sea ice, like average polar bear movements, however, are of limited value. During this study, we observed pulses in both easterly and westerly directions, during which ice moved at up to 2 km/h for periods as long as 3 or 4 days. Calculating short-term movement rates for polar bears is clearly not a simple matter. Therefore, comparisons with terrestrial animals and among polar bear populations living where the volatility of substrata differs must be made carefully.

Movement rates appeared to be at least somewhat influenced by reproductive status. We anticipated that movement rates of adult female bears would be low when their cubs were very young and increase as the cubs' mobility increased with age. In the SBS, movement rates of females with cubs were lower than those of other females. Also, the movement patterns of females accompanied by mobile yearlings and 2-year-olds were similar to those of solitary females.

The movement rate was dependent on month in the SBS. We predicted that movement rates and distances moved would be large in spring, when many bears hunt for seals in subnivalian lairs (Stirling and Latour 1978), and smaller in summer and fall, when lairs are not available. Contrary to our predictions, however, movement rates generally were low in autumn and spring and higher in summer (Tables 2, 3). Movement rates might be tied to the pace of change in the pack-ice environment, as well as to ice-movement vectors. Bears had the highest movement rates in June and July, when the sea ice was thawing and unconsolidated. SBS and NBS bears also had high movement rates in early winter, when ice is rapidly consolidating. Low movement rates in autumn and spring may indicate concentrated hunting with minimal travel between hunting sites.

Our observations differed from those made by Messier et al. (1992). They reported that peak movement rates of instrumented polar bears in Viscount Melville Sound (VMS) within the Canadian Arctic Archipelago, occurred from May

**Table 10.** Sizes (km<sup>2</sup>) of annual activity areas of female polar bears radio-collared in the southern ( $N = 75$ ) and northern ( $n = 29$ ) Beaufort seas, 1985–1995.

	Southern Beaufort Sea			Northern Beaufort Sea		
	Harmonic mean method		Convex polygon	Harmonic mean method		Convex polygon
	95%	50%		95%	50%	
Mean	149 465	18 795	166 694	76 696	10 525	86 205
Minimum	12 730	1 553	14 440	7 264	47	11 610
Maximum	596 800	60 810	616 800	201 200	43 590	271 700
SD	128 820	13 544	133 769	49 726	9 538	58 693
5% quantile	36 190	3 147	33 790	10 410	167	17 380
25% quantile	66 870	8 965	73 030	43 880	3 160	41 750
Median	104 600	13 720	134 500	68 570	8 569	74 710
75% quantile	188 000	25 220	210 000	113 300	13 490	115 900
95% quantile	493 400	60 810	475 500	167 100	28 250	210 400

**Note:** Areas within 95 and 50% contours surrounding observed points are shown for the harmonic mean method (Dixon and Chapman 1980). Convex polygon (100%) area estimates are shown for comparison with other studies.

**Table 11.** Sizes (km<sup>2</sup>) of annual activity areas of female polar bears varying in reproductive status that were radio-collared in the Beaufort Sea, 1985–1995.

	Southern Beaufort Sea			Northern Beaufort Sea		
	Mean	SE	$N$	Mean	SE	$N$
Harmonic mean (95%) activity areas						
Solitary females	173 026	19 381	45	96 228	21 278	6
Females with cubs	95 379	33 624	12	99 621	14 152	11
Females with yearlings	162 397	36 263	13	77 526	14 207	5
Harmonic mean (50%) activity areas						
Solitary females	21 917	1 915	45	15 860	6 189	6
Females with cubs	12 891	2 869	12	13 701	2 145	11
Females with yearlings	19 156	4 564	13	9 626	1 356	5
Convex polygon (100%) activity areas						
Solitary females	194 934	18 670	45	107 930	27 709	6
Females with cubs	100 423	36 283	12	105 081	19 322	11
Females with yearlings	168 232	44 933	13	81 924	13 584	5

**Note:** Areas within 95 and 50% contours surrounding observed points are shown for the harmonic mean method (Dixon and Chapman 1980). Convex polygon (100%) area estimates are shown for comparison with other studies.

to July, and that movement rates, although increasing after January, were low from October to March. We also observed high movement rates in summer, apparently because of rapidly changing ice conditions. In VMS, this activity may correspond to the peak feeding period. In both SBS and NBS areas, however, movement rates remained high in November and December, and were low in May. Messier et al. (1992) reported increasing mobility from January through spring in the Canadian Arctic, while we observed nearly the opposite trend. Further, overall movement rates reported for VMS were much lower than we observed. The peak movement rate of 0.46 km/h recorded by Messier et al. (1992, Table IV) was only a fraction of the highest rates we observed (Tables 1–3).

The lower level of winter movement among polar bears in VMS may be a consequence of the prevalence of multiyear ice in that area (Gloersen et al. 1992; Messier et al. 1992). The density of ringed seals is lower there than in most other

areas of polar bear habitat from Alaska through to western Greenland (Stirling and Øritsland 1995), and seals that are present in VMS tend to be more concentrated along the tidal cracks and pressure ridges that run parallel to the island coastlines (Kingsley et al. 1985). By comparison, the annual ice that predominates in most of the SBS is more dynamic and allows more sunlight into the water column to support primary productivity. This facilitates access to air for seals to breathe, and supports higher densities and numbers of both ringed seals and polar bears (Stirling et al. 1982; Kingsley et al. 1985; Stirling and Øritsland 1995). Polar bears are more abundant in the SBS, at least partly because of the greater foraging opportunities provided by active ice during the winter months. Polar bears in the Beaufort Sea may spend more time actively foraging, and those in the VMS area may spend more time resting and conserving energy. Messier et al. (1992) reported that long periods of “sheltering” were common among bears wintering in VMS,

**Table 12.** Monthly activity area sizes (km<sup>2</sup>) of radio-collared female polar bears in the southern and northern Beaufort seas, 1985–1996.

Month	Females with cubs			Solitary females			Females with yearlings			Females with 2-year-olds			Monthly total			Significantly different at $P = 0.05$
	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	Mean	SE	<i>N</i>	
Southern Beaufort Sea																
March				2792	1718	3	431	191	4	372	187	4	1053	531	11	
February							2641	824	4	586	211	6	1408	467	10	
April	344	110	9	2284	665	13	2459	1365	8	1078	348	6	1637	404	36	
October	1402	549	7	2591	660	15	1616	667	8				2053	398	30	
August	265	83	4	2795	615	18	1534	608	7				2142	438	29	
January							3149	2616	7	1007	430	5	2256	1519	12	
September	1189	763	2	2550	791	17	1989	1478	4				2334	631	23	
May	1193	351	8	2784	709	38	2079	576	12				2419	485	58	
July	1604	987	4	1672	282	23	5291	2900	9				2569	770	36	
June	172	59	5	2777	539	30	4689	2293	6				2739	533	41	
November	4970	1761	9	2591	656	10	5304	2901	11				4299	1190	30	
December	9760	4105	7				7588	3659	9				8538 <sup>a</sup>	2654	16	
Total	2658	712	55	2539	235	167	3516	671	89	786	160	21				
Northern Beaufort Sea																
April	116		1				501		1				309	192	2	
February							312	257	2				312	257	2	
December	606	232	4				221	39	3				441	147	7	
March							501	194	6				501	194	6	
November	597	100	5				1380	546	3				891	237	8	
January							983	786	6	767	734	3	911	551	9	
October	1428	513	8	2158		1	88		1				1367	435	10	
August	1094	732	7	217	208	2	2698	2091	5				1542	818	14	
September	1859		1				2067	507	2				1997	300	3	
May	1861	751	10	4643	2274	5	798	421	6				2220	694	21	
July	1863	761	10	405	187	3	7484	7166	2				2321	1027	15	
June	3896	1390	2	1806		1	1407		1				2751	875	4	
Total	1490	274	48	2403	1069	12	1413	476	38	767	734	3				

**Note:** Activity areas were calculated with 95% harmonic mean contour (Dixon and Chapman 1980) using  $\geq 8$  locations per month. In the southern Beaufort Sea, areas occupied in December were larger than those occupied in all other months. Other differences among months and differences among reproductive-status categories were not significant. Vertical lines in the last column overlap months for which data did not differ significantly.

<sup>a</sup> $F_{[11]} = 2.61, P = 0.004$ ; HSD = 4.67, df = 249,  $P = 0.05$ .

**Table 13.** Fidelity of satellite-radio-collared female polar bears to monthly activity areas in the Beaufort Sea, 1985–1995.

	Mean	<i>N</i>	SE	Significance
<b>Southern Beaufort Sea</b>				
July	199	78	17	
August	250	73	20	
May	267	122	22	
September	284	68	19	
June	292	106	28	
April	321	118	24	
February	353	27	50	
October	359	62	24	
November	384	76	29	
January	399	34	50	
December	404	49	42	
March	418	50	35	
<b>Northern Beaufort Sea</b>				
August	135	31	18	
July	147	30	26	
September	170	29	20	
June*	199	33	29	
October	196	20	33	
May	210	36	29	
November	242	19	38	
December	267	14	44	
January	294	14	50	
April	319	33	37	
February	362	15	52	
March	393	16	66	

**Note:** Distances (km) are separations of activity centers, calculated by harmonic mean, among years. In the southern Beaufort Sea, fidelity to monthly activity areas was greatest in July and least in March ( $F_{[11]} = 7.84$ ,  $P < 0.001$ ; HSD = 4.64,  $df = 785$ ,  $P = 0.05$ ). In the northern Beaufort Sea, fidelity to monthly activity areas was greatest in August and least in March ( $F_{[11]} = 6.38$ ,  $P < 0.001$ ; HSD = 4.66,  $df = 261$ ,  $P = 0.05$ ). Vertical lines in the last column overlap months for which data did not differ significantly.

\*The significance pattern in the northern Beaufort Sea for June does not follow the relative value of its mean, apparently because of greater variation among measures in that month.

and attributed this behavior to the poor foraging conditions there. Another factor may be the greater predictability of foraging conditions in the stable ice of VMS. With less change in the character of the sea ice after freeze-up, polar bears may be able to determine the profitable hunting areas early on, and therefore minimize midwinter searching for good hunting areas. The constantly changing sea ice of the Beaufort Sea, however, may require major modifications of foraging strategy from month to month or even day to day during breakup, freeze-up, or periods of strong winds.

Using mark and recovery data, Lentfer (1983) reported a mean movement rate for polar bears on the sea ice of 10.7 km/day (0.45 km/h if 24-h days are used), with no variation among different sex and age groups. Garner et al. (1990) reported a mean movement rate of PTT-equipped polar bears in the spring of 0.6 km/h, with a peak rate of 1.7 km/h. Our mean short-term movement rates (1.8–2.1 km/h) exceeded previously reported values. The maximum short-term travel rates that we measured were nearly 5 times those previously recorded.

### Net monthly movements

At any one time, some radio-collared bears made net movements in all directions. Significant directional trends among SBS bears occurred only in May–August, when net movements were significantly northward, in October, when the bears moved south, and in January, when they moved east. These net movements, except in January, appeared to be correlated with general patterns of ice formation and breakup. Between May and August, the annual ice in the southern regions of the SBS is disintegrating (Gloersen et al. 1992, Fig. 3.1), and polar bears move north to the general area of the central SBS, where a mixture of multiyear and annual ice remains throughout the summer (Gloersen et al. 1992, Fig. 3.1; see Seasonal concentrations and philopatry). October is usually the month of freeze-up (later in the eastern Beaufort Sea in recent years) and is the first time in months when bears are able to hunt on freshly forming ice nearer to the coast, where seal densities are usually higher. They disperse east and west, parallel to the coast, as ice solidifies in November.

In the NBS, the northerly net movement in June and the southerly net movement in September coincide with the pattern of ice retreat and advance (Gloersen et al. 1992, Fig. 3.1). Stirling (1990) also reported north–south seasonal movements of polar bears. In June, the sea along the east coast of Banks Island is often ice-free or has minimal ice coverage (Gloersen et al. 1992, Fig. 3.1). By September, however, annual ice begins to form along the coast and the polar pack begins to move south. Instrumented bears were quick to respond to these changes.

Variation in net monthly movement did not explain all seasonal patterns of distribution. Plots of centers of monthly activity revealed that Beaufort Sea polar bears had an affinity for the central Beaufort Sea in summer and tended to disperse to the east and west by late winter (Amstrup 2000). Hence, although analyses of net monthly movements suggested that trends in movement were mainly north–south, radio-collared polar bears that were in the eastern portions of the Beaufort Sea in spring returned west in summer. Likewise, bears that had moved into the Chukchi Sea in winter returned to the east in summer. Lentfer (1972, 1974, 1983) reported that polar bears moved significantly to the east in spring. Our observations indicated that such movements were representative of only some individuals and not the population (Tables 6, 7).

### Total distances

Lentfer (1983), Schweinsburg et al. (1981), and Stirling et al. (1980, 1984) reported from mark and recovery locations that distances moved by animals of different sex and age classes did not vary. Although sample sizes were small in those studies, and the main focus was on differences between males and females, the authors' findings were consistent with our observation of similarity in total movements of adult female bears of different reproductive categories. Until we are able to instrument young growing polar bears and adult males, we will be unable to quantitatively compare the movements of adult females with those of bears of other age and sex classes.

Garner et al. (1990) reported that the mean annual movement of 6 PTT-equipped polar bears in the Chukchi Sea was

5542 ± 634 km (mean ± SE). Our mean values (2360–3917 km/year for the NBS and SBS, respectively) were lower. To maintain contact with the sea ice, which fluctuates in seasonal extent, polar bears in the Chukchi and Bering seas must make extensive seasonal north–south movements corresponding with ice availability (Garner et al. 1990, 1994). The amount of annual fluctuation in the pattern of breakup and freeze-up in the SBS is less than that documented in the Chukchi Sea but more than that in the NBS (Gloersen et al. 1992), which probably explains the decline from west to east in the magnitude of the mean annual movements undertaken by female polar bears.

The largest and smallest total distances moved and net movements each month were highly concordant (Tables 4, 5, 8, 9). Both measures were highest in November for SBS bears and in May for NBS bears. Likewise, low values for both measures were in March and December for the SBS and NBS, respectively. The rankings of total and net movements for most other months, however, did not correspond closely. Nor did they correspond to monthly movement rates (Tables 2–5). Movement rate and net movement, it appears, need not correspond. The lack of concordance among different movement measures suggests that further studies are necessary to determine what information different measures convey, the relationships between those measures, and more generally, how polar bears utilize their environment. Also, this lack of concordance mandates care when comparing the results of different studies that may have used varying, and perhaps noncomparable, methods of assessing animal movements.

## Spatial-use patterns

### Activity areas

The areas of annual activity of Beaufort Sea polar bears were large and variable (Tables 10, 11), reflecting, as did other measurements, the great mobility of this species. Areas of monthly activity were also large. Neither rates nor linear measures of movement were consistent predictors of activity-area size (Table 12). Polar bears apparently can be highly mobile and yet confine their movements to areas already occupied. Solitary females are unencumbered by cubs and must build up their energy reserves to prepare for the birth of their next litter. Hence, we expected that they might utilize the largest activity areas. We also predicted that areas occupied by female polar bears would increase with the age of cubs. These predictions were largely confirmed. However, the great variability among individual bears made the significance of differences among reproductive classes difficult to assess.

Because polar bears catch seals mainly by still-hunting (Stirling and Latour 1978), we expected that the volatile summer and fall ice would minimize the predictability of seal-hunting opportunities. This would necessitate larger activity areas than during winter and spring. Hence, we predicted that monthly activity areas would be larger for all classes of bears in summer and fall than during other times of the year. This prediction seemed to be upheld in the SBS, where the largest monthly activity areas were measured during June–July and November–December. These were also the months of highest movement rates. In the NBS, movement rates and activity areas in June and July were also

large. Unlike those in the SBS, however, bears in the NBS were not highly mobile in autumn and early winter.

The labile nature of the sea ice causes annual variability in the distribution of suitable habitat for seals (DeMaster et al. 1980; Stirling et al. 1982; Stirling and Øritsland 1995). Thus, unlike some terrestrial bears, female polar bears derive no benefit from defending territories. The location of resources is less predictable than that of many terrestrial resources, and they tend to be distributed at low densities over very large areas. Hence, the distribution of female bears among years is variable. Males, similarly, would need to be free of the need to defend territories if they are, each year, to maximize their potential for finding mates (Ramsay and Stirling 1986).

Annual activity areas of females monitored for multiyear periods did show, however, that the size of new area occupied in each additional year of monitoring varied. Also, for most animals, there was a “core area” of overlap each year (Fig. 2). This observation suggests that activity areas of polar bears, when viewed over multiyear periods, might be called home ranges. A large activity area, or home range, of which only a portion may be used in any one season or year may be an important strategy for life on the variable pack ice (Ferguson et al. 1999).

Linear movements and activity areas in the Beaufort Sea may be intermediate in magnitude between those reported for polar bears in the Chukchi Sea and those reported from bears in parts of the Canadian Arctic Archipelago (Schweinsburg and Lee 1982; Messier et al. 1992). PTT-equipped polar bears in the Chukchi Sea occupied average annual activity areas of 244 463 km<sup>2</sup> (Garner et al. 1990). Schweinsburg and Lee (1982) reported maximum activity areas of <23 000 km<sup>2</sup> and hypothesized that movements of polar bears are inversely proportional to body stature and habitat richness. Seasonal and annual variability in sea-ice cover and character, and the resulting variation in availability of prey, may overshadow considerations of habitat richness, however. Polar bears from the Beaufort and Chukchi seas appear to be at least as large as those in the High Arctic (Wilson 1976). Further, the sea ice of the Chukchi and Beaufort seas is more dynamic and unpredictable than the ice of the Canadian archipelago (Garner et al. 1990, 1994; Gloersen et al. 1992). The mobility of polar bears appears to relate to this variability.

Observations made during this study indicate that polar bears are among the most mobile of quadrupeds. Yet rates of oxygen consumption by two polar bears walking on treadmills indicated that they were energetically inefficient walkers (i.e., they used more energy for locomotion than other mammals of a comparable size). Øritsland et al. (1976) and Hurst et al. (1982a, 1982b) attributed inefficient walking to aspects of polar bear morphology, specifically the massive forelimbs that have evolved for capturing prey. Economy of transport, they suggested, was compromised by considerations of thermoregulation and hunting strategy. Chassin et al. (1976) reported similar results and conclusions from studies of male lions, which also have massive forelimbs. In contrast, Taylor et al. (1974) found that differing configurations and masses of limbs among a variety of mammals had little effect on relative costs of locomotion. Studies of the costs of locomotion among a diverse group of herbivores,



including domesticated animals (which are largely insulated from natural selection for mobility), gave similar results (Fancy and White 1985). The great mobility we observed during this study suggests that the pressure of natural selection on polar bears to walk in an energetically efficient manner must have been significant. How, then, could they be inefficient walkers?

Relationships between polar bears and their ringed seal prey further complicate this issue. Two independent studies of regions where population-size estimates are available for both polar bears and ringed seals have shown that the number of ringed seals present in an area correlates well with the number required to meet the energetic needs of the bears resident there (Stirling and Øritsland 1995; Kingsley 1998). Possible differences in the amount of travel required for bears foraging in different geographic areas were not considered. Yet across the range of populations reviewed, field metabolic rates (approximately twice the basal metabolic rate as calculated by Kleiber (1961)) for bears of various sizes, suggested a conservative agreement between energetic requirements of the bears and the numbers of seals required to support them (Stirling and Øritsland 1995). The variation, among polar bear populations, in the extent of annual movements, and the hypotheses regarding their energetic requirements suggest that further research on locomotion of polar bears and ecological relationships with their prey may be a rewarding area for future research.

#### *Philopatry*

Polar bears live a long time, and success in exploiting the environment should be enhanced by knowledge gained from previous experiences. Amstrup and Gardner (1994) reported that maternal polar bears in the Beaufort Sea were faithful to a denning substrate and to a general geographic area, but not to specific den sites. Movements of nonpregnant bears also indicate a pattern of regional and seasonal fidelity. Nonpregnant bears, which do not den for the winter, were most faithful to summering areas and least faithful to feeding areas of late winter and spring. Our observations differed from those of Stirling et al. (1980, 1984), Schweinsburg et al. (1981), and Lentfer (1983), which suggested great fidelity to late-winter and spring feeding and breeding areas.

Polar bears in Manitoba return each summer to the same stretch of the Hudson Bay coastline (Stirling et al. 1977; Derocher and Stirling 1990). Although this pattern is strongly influenced by the annual patterns of breakup and freeze-up of annual ice in Hudson Bay, recent studies indicate that individual bears show a high degree of fidelity to specific coastal areas regardless of where the last ice melts (Stirling et al. 1999). Similarly, the distribution of ice in the Beaufort Sea is most constrained in summer, the time when polar bears showed the greatest degree of fidelity. As summer progresses, the ice in the Beaufort Sea retreats to the north. Breakup occurs first and most rapidly at the eastern and western ends of the SBS. By midsummer the most stable ice in the SBS is in the central portion offshore from Lonely to the Canadian border (Gloersen et al. 1992, Fig. 3.1). Satellite-radio-collared bears returned to that area every summer. Hence, although there are no geographic barriers to movement out of the Beaufort Sea, a relatively discrete

subpopulation there may be maintained as a result of the general pattern of ice formation and ablation.

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#### **References**

- Amstrup, S.C. 2000. Polar bear. *In* The natural history of an oil field: development and biota. *Edited by* J.C. Truett and S.R. Johnson. Academic Press, San Diego. pp 133–157.
- Amstrup, S.C., and DeMaster, D.P. 1988. Polar bear *Ursus maritimus*. *In* Selected marine mammals of Alaska: species accounts with research and management recommendations. *Edited by* J.W. Lentfer. Marine Mammal Commission, Washington, D.C. pp. 39–56.
- Amstrup, S.C., and Durner, G.M. 1995. Survival rates of radio-collared female polar bears and their dependent young. *Can. J. Zool.* **73**: 1312–1322.
- Amstrup, S.C., and Gardner, C. 1994. Polar bear maternity denning in the Beaufort Sea. *J. Wildl. Manage.* **58**: 1–10.
- Bethke, R., Taylor, M.K., Amstrup, S.C., and Messier, F. 1996. Population delineation of polar bears using satellite collar data. *Ecol. Appl.* **6**: 311–317.
- Biondini, M.E., Mielke, P.W., Jr., and Redente, E.F. 1988. Permutation techniques based on Euclidean analysis spaces: a new and powerful statistical method for ecological research. *Coenoses*, **3**: 155–174.
- Chassin, P.E., Taylor, C.R., Heglund, C., and Seeherman, H.J. 1976. Locomotion in lions: energetic cost and maximum aerobic capacity. *Physiol. Zool.* **49**: 1–10.
- DeMaster, D.P., and Stirling, I. 1981. *Ursus maritimus*. *Mamm. Species No.* 145. pp. 1–7.
- DeMaster, D.P., Kingsley, M.C.S., and Stirling, I. 1980. A multiple mark and recapture estimate applied to polar bears. *Can. J. Zool.* **58**: 633–638.

- Derocher, A.E., and Stirling, I. 1990. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. *Can. J. Zool.* **68**: 1395–1403.
- Dixon, K.R., and Chapman, J.A. 1980. Harmonic mean measure of animal activity areas. *Ecology*, **6**: 1040–1044.
- Environmental Systems Research Institute (ESRI). 1992. Map projections and coordinate management. ARC/INFO user's guide. Environmental Systems Research Institute, Inc., Redlands, Calif.
- Fancy, S.G., and White, R.G. 1985. Incremental costs of activity. *In* Bioenergetics of wild herbivores. *Edited by* R.J. Hudson and R.G. White. CRC Press, Boca Raton, Fla. pp. 145–157.
- Fancy, S.G., Pank, L.F., Douglas, D.C., Curby, C.H., Garner, G.W., Amstrup, S.C., and Regelin, W.L. 1988. Satellite telemetry: a new tool for wildlife research and management. U.S. Fish Wildl. Serv. Resour. Publ. No. 172.
- Ferguson, S.H., Taylor, M.K., Rosing-Asvid, A., Born, E.W., and Messier, F. 1999. Determinants of home range size in polar bears. *Ecol. Lett.* **2**: 311–318.
- Ferguson, S.H., Taylor, M.K., Born, E.W., and Messier, F. 1998. Fractals, sea-ice landscape and spatial patterns of polar bears. *J. Biogeogr.* **25**: 1081–1092.
- Garner, G.W., Knick, S.T., and Douglas, D.C. 1990. Seasonal movements of adult female polar bears in the Bering and Chukchi seas. *In* Bears—Their Biology and Management: Proceedings of the 8th International Conference on Bear Research and Management, Victoria, B.C., 20–25 February 1989. *Edited by* L.M. Darling and W.R. Archibald. International Association for Bear Research and Management, Washington, D.C. pp. 219–226. [Available from Michael R. Pelton, Department of Forestry, Wildlife, and Fisheries, The University of Tennessee, P.O. Box 1071, Knoxville, TN 37901-1071, U.S.A.]
- Garner, G.W., Amstrup, S.C., Stirling, I., and Belikov, S.E. 1994. Habitat considerations for polar bears in the North Pacific Rim. *Trans. North Am. Wildl. Nat. Resour. Conf.* **59**: 111–120.
- Gloersen, P., Campbell, W.J., Cavalieri, D.J., Comiso, J.C., Parkinson, C.L., and Zwally, H.J. 1992. Arctic and Antarctic sea ice, 1978–1987: satellite passive-microwave observations and analysis. *NASA Sci. Publ.* SP-511.
- Harington, C.R. 1968. Denning habits of the polar bear (*Ursus maritimus*). *Can. Wildl. Serv. Rep. Ser. No.* 5.
- Harris, R.B., Fancy, S.G., Douglas, D.C., Garner, G.W., Amstrup, S.C., McCabe, T.R., and Pank, L.F. 1990. Tracking wildlife by satellite: current systems and performance. U.S. Fish Wildl. Serv. Tech. Rep. No. 30.
- Hayne, D.W. 1949. Calculation of size of home range. *J. Mammal.* **39**: 1–18.
- Hayward, G.D., Hayward, P.H., and Garton, E.O. 1993. Ecology of boreal owls in the northern Rocky Mountains, U.S.A. *Wildl. Monogr.* No. 124.
- Hurst, R.J., Leonard, M.L., Watts, P.D., Beckerton, P., and Øritsland, N.A. 1982a. Polar bear locomotion: body temperature and energetic cost. *Can. J. Zool.* **60**: 40–44.
- Hurst, R.J., Øritsland, N.A., and Watts, P.D. 1982b. Body mass, temperature and cost of walking in polar bears. *Acta Physiol. Scand.* **115**: 391–395.
- IUCN/SSC Polar Bear Specialist Group. 1998. Polar bears. *In* Proceedings of the 12th Working Meeting of the IUCN/SSC Polar Bear Specialist Group. IUCN Species Survival Commission. Occas. Pap. No. 19.
- Kie, J.G., Baldwin, J.A., and Evans, C.J. 1996. CALHOME: a program for estimating animal home ranges. *Wildl. Soc. Bull.* **24**: 342–344.
- Kingsley, M.C.S. 1998. The numbers of ringed seals (*Phoca hispida*) in Baffin Bay and associated waters. *In* Ringed seals in the North Atlantic. *Edited by* M.-P. Heide-Jorgensen and C. Lydersen. The North Atlantic Marine Mammal Commission, Tromsø, Norway. pp. 181–196.
- Kingsley, M.C.S., Stirling, I., and Calvert, W. 1985. The distribution and abundance of seals in the Canadian High Arctic, 1980–1982. *Can. J. Fish. Aquat. Sci.* **42**: 1189–1210.
- Kleiber, M. 1961. The fire of life: an introduction to animal energetics. John Wiley and Sons, Inc., New York.
- Lair, H. 1987. Estimating the location of the focal center in red squirrel home ranges. *Ecology*, **68**: 1092–1101.
- Larsen, T. 1971. Capturing, handling and marking polar bears in Svalbard. *J. Wildl. Manage.* **35**: 27–36.
- Lentfer, J.W. 1972. Polar bear – sea ice relationships. *In* Bears—Their Biology and Management: Proceedings of the 2nd International Conference on Bear Research and Management, Calgary, Alta., 6–9 November 1970. *Edited by* S. Herrero. International Union for the Conservation of Nature and Natural Resources, Morgues, Switzerland (IUCN Publ. n.s. No. 23). pp. 165–171.
- Lentfer, J.W. 1974. Discreteness of Alaskan polar bear populations. *In* Proceedings of the 11th International Congress of Game Biologists, Stockholm, Sweden, 3–7 September 1973. *Edited by* I. Kjerner and P. Bjurholm. Swedish National Environment Protection Board, Stockholm. pp. 323–329.
- Lentfer, J.W. 1983. Alaskan polar bear movements from mark and recovery. *Arctic*, **36**: 282–288.
- Messier, F., Taylor, M.K., and Ramsay, M.A. 1992. Seasonal activity patterns of female polar bears (*Ursus maritimus*) in the Canadian Arctic as revealed by satellite telemetry. *J. Zool. (Lond.)*, **226**: 219–229.
- Mielke, P.W. 1991. The application of multivariate permutation methods based on distance functions in the earth sciences. *Earth-Sci. Rev.* **31**: 55–71.
- Mielke, P.W., Berry, K.J., Brockwell, P.J., and Williams, J.S. 1981. A class of nonparametric tests based on multiresponse permutation procedures. *Biometrika*, **68**: 720–724.
- Pedersen, A. 1945. Der Eisbär: Verbreitung und Lebensweise. E. Bruun, Copenhagen.
- Ramsay, M.A., and Stirling, I. 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *J. Zool. (Lond.)*, **214**: 601–634.
- Schoener, T.W. 1981. An empirically based estimate of home range. *Theor. Popul. Biol.* **20**: 281–325.
- Schweinsburg, R.E., and Lee, L.J. 1982. Movement of four satellite-monitored polar bears in Lancaster Sound, Northwest Territories. *Arctic*, **35**: 504–511.
- Schweinsburg, R.E., Furnell, D.J., and Miller, S.J. 1981. Abundance, distribution and population structure of polar bears in the lower central Arctic islands. Northwest Territories Wildlife Service Completion Rep. No. 2.
- Schweinsburg, R.E., Lee, L.J., and Haigh, J.C. 1982. Capturing and handling polar bears in the Canadian Arctic. *In* Chemical immobilization of North American wildlife. *Edited by* L. Nielsen, J.C. Haigh, and M.E. Fowler. Wisconsin Humane Society Inc., Milwaukee. pp. 267–289.
- Slauson, W.L., Cade, B.S., and Richards, J.D. 1991. User's manual for BLOSSOM statistical software. United States Fish and Wildlife Service, National Ecology Research Center, Fort Collins, Colo.
- Solow, A.R. 1989. A randomization test for independence of animal locations. *Ecology*, **70**: 1546–1549.
- Spencer, W.D., and Barrett, R.H. 1984. An evaluation of the harmonic mean measure for defining carnivore activity areas. *Acta Zool. Fenn.* **171**: 255–259.
- Stirling, I. 1990. Polar bears and oil: ecological perspectives. *In* Sea

- mammals and oil: confronting the risks. *Edited by* J.R. Geraci and D.J. St. Aubin. Academic Press, San Diego. pp. 223–234.
- Stirling, I., and Latour, P.B. 1978. Comparative hunting abilities of polar bear cubs of different ages. *Can. J. Zool.* **56**: 1768–1772.
- Stirling, I., and Øritsland, N.A. 1995. Relationships between estimates of ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) populations in the Canadian Arctic. *Can. J. Fish. Aquat. Sci.* **52**: 2594–2612.
- Stirling, I., Jonkel, C., Smith, P., Robertson, R., and Cross, D. 1977. The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay. *Can. Wildl. Serv. Occas. Pap. No.* 33.
- Stirling, I., Calvert, W., and Andriashek, D. 1980. Population ecology studies of the polar bear in the area of southeastern Baffin Island. *Can. Wildl. Serv. Occas. Pap. No.* 44.
- Stirling, I., Kingsley, M.C.S., and Calvert, W. 1982. The distribution and abundance of seals in the eastern Beaufort Sea, 1974–1979. *Can. Wildl. Serv. Occas. Pap. No.* 47.
- Stirling, I., Calvert, W., and Andriashek, D. 1984. Polar bear (*Ursus maritimus*) ecology and environmental considerations in the Canadian High Arctic. *In* Northern ecology and resource management. *Edited by* R. Olson, F. Geddes, and R. Hastings. University of Alberta Press, Edmonton. pp. 201–222.
- Stirling, I., Spencer, C., and Andriashek, D. 1989. Immobilization of polar bears (*Ursus maritimus*) with Telazol in the Canadian Arctic. *J. Wildl. Dis.* **25**: 159–168.
- Stirling, I., Lunn, N.J., and Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic*, **52**: 294–306.
- Swihart, R.K., and Slade, N.A. 1985a. Testing for independence of observations in animal movements. *Ecology*, **66**: 1176–1184.
- Swihart, R.K., and Slade, N.A. 1985b. Influence of sampling interval on estimates of home-range size. *J. Wildl. Manage.* **49**: 1019–1025.
- Taylor, C.R., Shkolnik, A., Dmiel, R., Baharav, D., and Borut, A. 1974. Running in cheetahs, gazelles, and goats: energy cost and limb configuration. *Am. J. Physiol.* **227**: 848–850.
- Wilson, D.E. 1976. Cranial variation in polar bears. *In* Bears—Their Biology and Management: Proceedings of the 3rd International Conference on Bear Research and Management, Binghamton, N.Y., 31 May – 1 June 1974, and Moscow, USSR, 11 June 1974. *Edited by* M.R. Pelton, J.W. Lentfer, and G.E. Folk, Jr. International Union for the Conservation of Nature and Natural Resources, Morgues, Switzerland (IUCN Publ. n.s. No. 40). pp. 477–453.
- Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice Hall, Inc. Englewood Cliffs, N.J.
- Øritsland, N.A., Jonkel, C., and Ronald, K. 1976. A respiration chamber for exercising polar bears. *Norw. J. Zool.* **24**: 65–67.